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Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960–88

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Abstract—Changes in winter and spring mixed layer depths in the North Pacific on decadal and basin scales affect biological production. In the subtropical and transition zones these depths were 30–80% greater during 1977–88 than during 1960–76; in the subarctic zone they were 20–30% shallower. We attribute these changes to an intensification of the Aleutian Low Pressure System. A deeper mixed layer might increase phytoplankton production in nutrient-poor regions by supplying more deep nutrients; it might decrease production in light-poor regions by mixing cells into darker water. A plankton population dynamics model suggests that a deeper subtropical mixed layer and a shallower subarctic mixed layer both would increase primary and secondary production by about 50%, and these increases were found not to be very sensitive to model parameter values; in the transition zone, however, the predicted change in production was smaller and more sensitive to changes in model parameters. Increases in higher tropic levels have been observed in subtropical and subarctic zones during 1977–88. This is consistent with model results and the idea that the subtropical zone is nutrient-poor, the subarctic zone is light-poor, and the transition zone is not consistently limited by any one thing. Further, our results show changes in mixed layer depths occur on decadal and basin scales and may be an important mechanism linking variation in the atmosphere and oceanic ecosystem productivity.

INTRODUCTION

The Aleutian Low Pressure System is the dominant meteorological feature in the winter and spring North Pacific atmosphere and has strong links to North Pacific oceanography (Namias, 1969). Changes in production of fisheries have been linked to the strength of this system (Polovina *et al.*, 1994; McFarlane and Beamish, 1992; Beamish and Bouillon, 1993; Brodeur and Ware, 1992). Obvious pathways for these effects are changes in cloud cover, upper water temperature and, especially, mixed layer depth, influencing the production of plankton and therefore the whole oceanic food web. Interannual variation in mixed layer depth (MLD) is often cited as the mechanism which enables atmospheric variation to produce biological variation in oceanic ecosystems (Polovina *et al.*, 1994; Venrick *et al.*, 1987; Dickson *et al.*, 1988; Steele and Henderson, 1993; Mann, 1993). A deeper mixed

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layer might increase phytoplankton production, by supplying more deep nutrients; or it might decrease it, by mixing cells into darker water. However, most studies use wind or atmospheric pressure as proxies for MLD and develop a qualitative rather than quantitative link between interannual variation in MLD and biological production.

A North Pacific climate event characterized by an intensification of the Aleutian Low Pressure System occurred during 1977–88 (Graham, 1994; Trenberth and Hurrell, 1994). In this paper we take advantage of this decadal variation in the strength of Aleutian Low. It is thought that it caused changes in the wind stress distribution and strength, and thus is the depth of the mixed layer. The latter, which is of direct interest in the present study, is actually easier to compute from the available data. We compute MLD for the central and North Pacific during two decadal periods differing in the mean intensity of the Aleutian Low. We show that major regional changes in mean MLD occurred between these periods.

To examine the effects on biological production, we use a model of the population dynamics of the lowest trophic levels, phytoplankton and herbivorous zooplankton, as affected by nutrient and light levels. We observe the changes in abundance and production predicted by the model at different latitudes, between the 1960–76 and 1977–88 average MLD patterns. We might expect that reactions to changes in MLD, in both real and model ecosystems, would be clear in regions where there is a clear limiting factor, either light or nutrients. In regions where both limitations are about equal, we would expect the reaction of both real and model ecosystems to be confused, and sensitive to more subtle effects. As a proxy for experimenting with different model structures, we investigate how the sensitivity to changes in MLD depends on some of the model parameters that determine the nutrient and light levels. Finally, we examine reports from the fisheries literature of changes at higher trophic levels.

COMPUTATIONS

Mixed layer depth

Vertical temperature profile data from NODC were used to estimate MLD. The NODC data set contains profiles from a variety of instruments, including bathythermographs (both mechanical and expendable), CTDs and STDs. The MLD was estimated independently for each temperature profile. Only profiles which begin within 25 m of the surface were used. Attention focused on the upper 400 m of the temperature field because our main interest was in identifying wind-mixing events rather than the seasonal heating changes that can extend significantly deeper.

Mixed layer is an arbitrary concept, and a single, universally accepted, definition of MLD does not exist. We developed two algorithms that effectively define MLD as the depth of a surface layer in which the vertical temperature gradients are much smaller than are observed deeper in the water column. The first algorithm used a least squares criterion to identify the depth of the layer that could be described by a zero gradient; the second estimates the gradient profile itself and defines MLD on the basis of the magnitude of the computed gradient. The first algorithm was found to be less sensitive to the vertical distribution of data points comprising a particular profile, and was chosen as the primary algorithm. That is, for each profile, the first algorithm was attempted. If it failed, then the second was tried. If the second failed, no MLD or mixed layer temperature (MLT) estimate was made for that profile.

The two algorithms, and the criteria for which they failed, were simple. The first algorithm required that there be at least four data points in the upper 50 m of the water column. This algorithm approximated the thermal structure as a constant temperature layer of thickness (MLD) that is joined to a linearly decreasing function of temperature at greater depths. Thus, there are three parameters: MLT, MLD and the temperature gradient below the mixed layer. The parameters are estimated by a least squares fit to the observed temperature versus depth data. The model is nonlinear, and the parameters were estimated by doing a simple comprehensive search through parameter space.

If a profile had fewer than four observations within the top 50 m, then the first algorithm failed and the second method, which was based on the vertical temperature gradient, was attempted. In this method temperature data were interpolated to a fine depth grid with a cubic spline, and the interpolated temperature function was used to estimate the temperature gradient as a function of depth by finite differencing. Profiles with temperature inversions leading to unstable gradients greater than 0.1° K/m indicated problems with the spline interpolation, and these profiles were rejected. For the remaining profiles, the MLD was estimated as the shallowest depth where the magnitude of the temperature gradient exceeded 0.04° K/m.

After the MLD was estimated, values less than 10 m were rejected because the profiles do not resolve structure on such small scales. Also, MLD values greater than 75% of the depth range covered by the profile were not allowed. It was observed that an MLD value of 300 m occurred more frequently than did values of just less than or greater than 300 m. This is because a large fraction of the profiles are from expendable bathythermographs that typically reach depths of approximately 400 m. This observation raised a concern that the distribution in time and space of different instrument types used for the profiles may bias our estimates of MLD. For example, the older mechanical bathythermographs (MBT) often sampled only down to 100 m. If these MBT measurements were dominant in some spatial-temporal area, then the MLD would be observed only when it was rather small. Other instrument-related biases also concerned us. For example, CTD measurements are often not taken during heavy weather, which is likely correlated with deepened mixing. Thus CTD data may bias MLD estimates to low values as well. To check the importance of these instrument-related biases, we checked the MLD estimates shown in the next section against estimates made using only MLD values estimated for XBT data. The spatial patterns of increased or decreased MLD between the two time periods described in the next section were relatively unchanged.

The MLD results from the automated algorithms were directly verified for nearly 5000 profiles chosen at random. This was done by plotting the temperature versus depth data along with the estimated MLD and MLT. We also examined the mean seasonal cycles and histograms of the MLD and MLT in various regions. The results of these checks convinced us that the MLD and MLT data sets were basically sound; however, it is important to approach the data set statistically. It is also important to check the robustness of any derived quantities. For example, the quarterly mean MLD values discussed in the next section were checked by comparing them to median values, trimmed mean values and values computed over different geographical ranges.

Generally, temporal and spatial density of vertical temperature data was not sufficient to construct annual MLD time series. Instead we compared changes in MLD, between the period 1960–76, when the Aleutian Low was close to its average level and 1977–88, when the Aleutian Low was intensified (Fig. 1). The spatial distribution of vertical profile

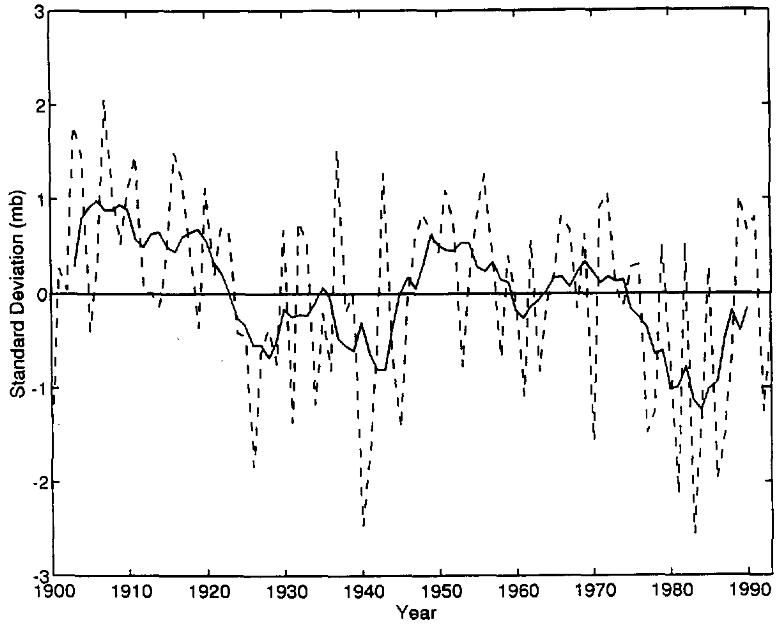


Fig. 1. Normalized sea level pressure November–March (30°–65°N, 160°E–140'W). Solid line is 7 yr moving average (Data from NCAR).

stations shows complete central and North Pacific coverage with the heaviest sampling along regular ship tracks (Fig. 2). To compare changes in mean quarterly MLD between the decadal periods, we first computed the mean quarterly MLD, pooling all data for each decadal period in squares of 2° of longitude and latitude over the central and North Pacific. Then the percent change in quarterly MLD between the two periods relative to 1960–76 MLD was calculated for each 2° square as the difference between quarterly MLD (1977–88) and quarterly MLD (1960–76) divided by quarterly MLD (1960–76) × 100%. If different quarters showed similar changes between the two periods a seasonal change covering the combined quarters was computed as the average of the quarterly changes. Contour plots of the percent change in MLD and change in °C MLT were constructed to show spatial patterns.

We examine MLD changes in three regions, the Northwestern Hawaiian Islands (NWHI) (25–30°N, 175°E–165°W), Emperor Seamounts (30–45°N, 160°E–170°W), and the Gulf of Alaska (50–60°N, 140–170°W), where substantial MLD changes are seen and where ecosystem changes have been observed. For these three regions, monthly MLD and MLT were computed for each decadal period as the monthly mean within the spatial box defining each region.

Plankton model

Our objective for using a plankton model is to quantify the impacts on biological production of interdecadal variations in MLD, and this requires quantifying impacts due to changes in light and nutrients. We've chosen the simplest model capable of addressing

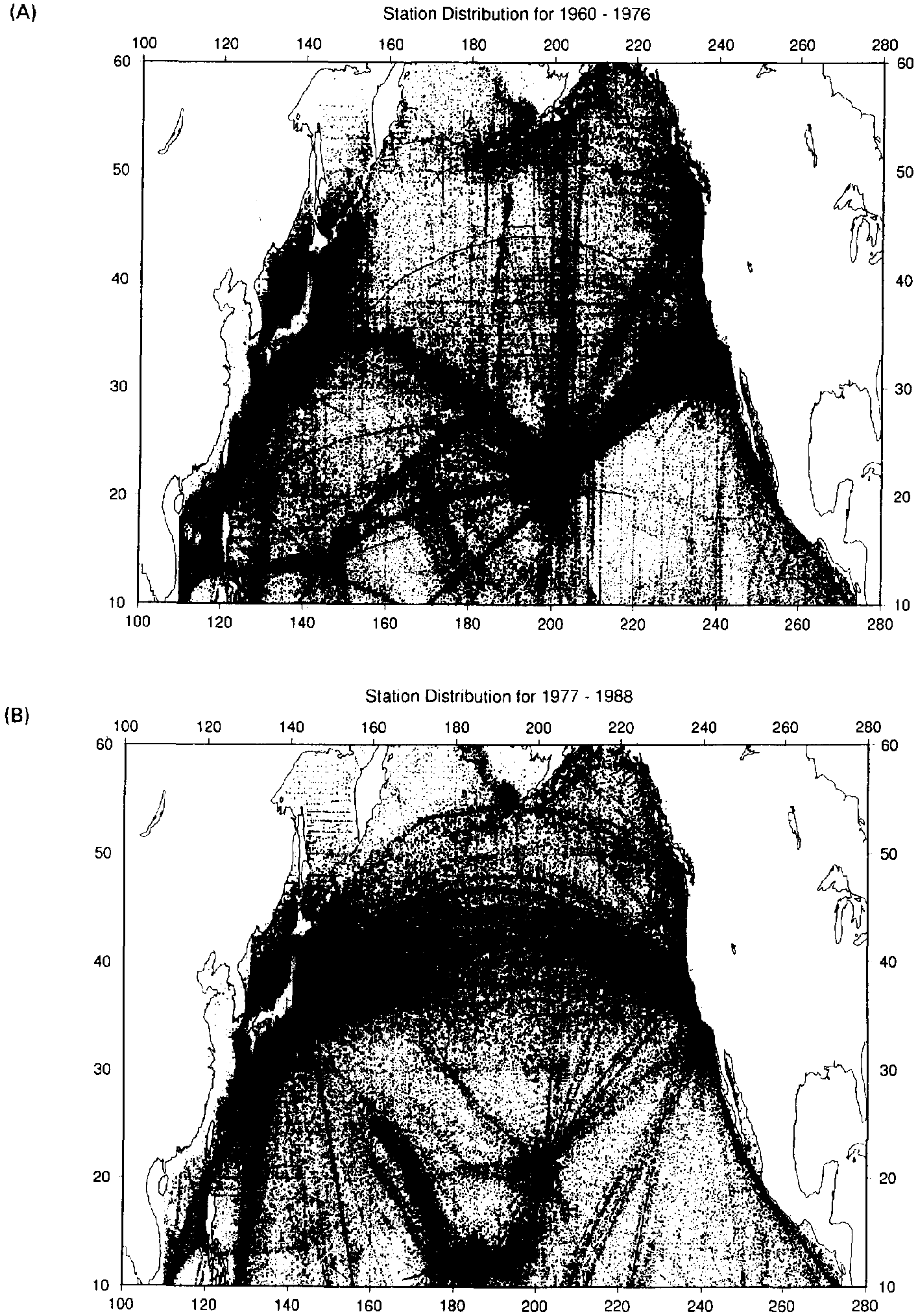


Fig. 2. Spatial distribution of NODC vertical temperature stations. (A) stations from 1960–76; (B) stations from 1977–88.

these impacts: the Evans and Parslow (1985) model of nitrate, phytoplankton and herbivorous zooplankton. The vertical structure is described as an upper mixed layer containing nutrients and plankton whose concentration does not change with depth within the layer, and a lower layer with nutrients but no plankton. The assumption that no plankton are found below the mixed layer is likely to be unrealistic for shallow MLD in the summer but more realistic during deep winter and spring MLD, which is the period we will subsequently show to contain the decadal variation.

The Evans and Parslow (1985) model formulation assumes that the density of nutrients below the MLD is constant, independent of MLD. However, nitrate-by-depth data (from Ocean Climate Lab, NODC) pooled over season and year for the NWHI, Emperor Seamounts and Gulf of Alaska show nitrate densities for all three regions and increase approximately linearly with depth. Thus, we use the approach of Steele and Henderson (1993) and express the nitrogen density below the MLD as a function of MLD with the relationship for each region estimated from the nitrate at depth data (Table 1). The photosynthetic equation is described by two parameters, a low light photosynthetic slope and a maximum photosynthetic rate (Evans and Parslow, 1985). Following the approach used in a plankton model of the North Atlantic (Sarmiento *et al.*, 1993), the low light slope is assumed to be constant over space and time while the maximum photosynthetic rate (P_{max}) is expressed as a function of MLT (T (°C)) as:

$$P_{max} = 0.6(1.066)^{T} \tag{1}$$

All other parameter values for the model for the three regions are given in Table 1.

In principle we could run the model with the actual history of mixed layer depths for the period 1960–88 and record the year-to-year responses of biological variables, as in Evans and Pepin (1989) and Steele and Henderson (1993). In practice, however, there are not enough MLD data to force the model, and not enough biological data to check the results. Instead, we constructed average annual MLD and MLT cycles for two contrasting periods, 1960–76 and 1977–88, and compared the steady annual cycles of the model in response to these two steady cycles of driving variables. We plot the annual cycle for 1960–76, and then the annual cycle of the ratio of the 1977–88 and 1960–76 cycles.

The ratios we compute are for a particular model and a particular set of parameter values; we wish to know if they are stable under changes of model or parameters, and if the stability changes with region. Investigating stability under change of model would take us too far afield, but we did look at changing parameters. Because we are interested in the transition from light- to nutrient-poor regions, we changed the parameter group that determines the supply of light (cloudiness, attenuation coefficients of water and phytoplankton) or nutrients (base level and slope of subsurface nitrate) by 25% up or down, and recalculated the sensitivities of phytoplankton production to changes in mixed layer depth, at different latitudes. (Phytoplankton and zooplankton concentrations generally have the same trends as production: see Fig. 8.)

RESULTS

The largest change in MLD and MLT between the two periods occurs during winter and spring quarters when the Aleutian Low is dominant in the North Pacific circulation. The change in both winter and spring mean MLD and MLT between 1960–76 and 1977–88 shows the same regional pattern and, hence, we compute mean MLD and MLT changes

Table 1. Plankton model input parameters

Parameter	Units	NWHI		Emperor Seamounts		Gulf of Alaska	
		Value	Source	Value	Source	Value	Source
Deep nutrients	mmol m^{-3}	0.4 if MLD < 50 m; 0.4 + 0.035 * (MLD − 50) if MLD ≥ 50 m	(1)	2.0 + 0.5 * MLD	(1)	7.0 + 0.18 * MLD	(1)
Diffusion rate	$mday^{-1}$	0.7	(2)	0.7	(2)	0.7	(2)
Low light photosynthetic slope	$(Wm^{-2})^{-1}$ day^{-1}	0.14	(2)	0.14	(2)	0.14	(2)
Light attenuation due to water	m^{-1}	0.04	(3)	0.04	(3)	0.04	(3)
Light attenuation by phytoplankton	m^{-1}	0.03	(3)	0.03	(3)	0.03	(3)
Cloud cover	—	0.5		0.7	(4)	0.7	(4)
Nutrient uptake half saturation	mmol m^{-3}	0.5	(4)	0.5	(4)	0.5	(4)
Plant metabolic loss	day^{-1}	0.04	(3)	0.04	(3)	0.04	(3)
Sinking rate	$Mday^{-1}$	0.2	(5)	0.5	(5)	0.5	(5)
Herbivore grazing threshold	mmol m^{-3}	0.05		0.1	(4)	0.1	(4)
Herbivore grazing half saturation	mmol m^{-3}	1.0	(4)	1.0	(4)	1.0	(4)
Maximum herbivore grazing rate	day^{-1}	1.0	(4)	1.0	(4)	1.0	(4)
Herbivore grazing efficiency	—	0.75	(2)	0.75	(2)	0.75	(2)
Loss to carnivores	day^{-1}	0.05		0.07	(4)	0.07	(4)
Mean latitude	degrees	27.5		35.0		55.0	

Sources: (1) NODC, (2) Fasham, press 1995, (3) Sarmiento *et al.*, 1993, (4) Evans and Parslow, 1985, (5) Evans, 1988.

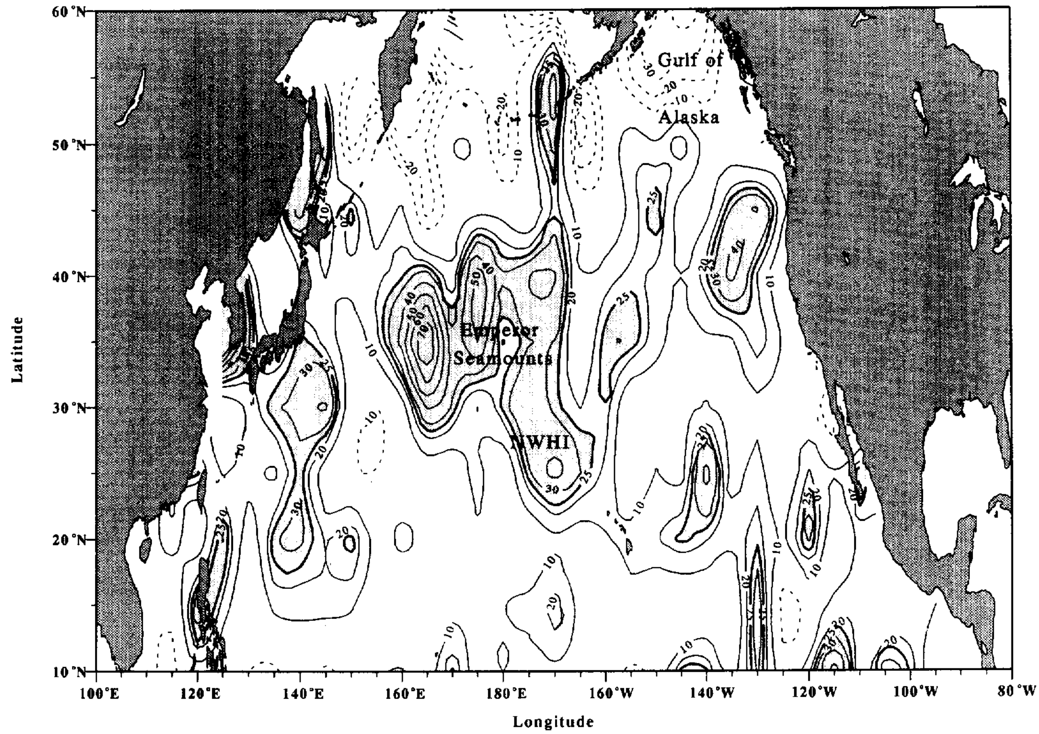


Fig. 3. Percent change in mean winter and spring MLD between 1977–88 and 1960–76 relative to 1960–76 levels. Shading for 1977–88 MLD which are more than 25% deeper than 1960–76 MLD. Dashed contours are negative values.

for the winter and spring periods (Figs 3 and 4). During winter and spring 1977–88 MLD was 30–80% deeper in the central North Pacific, centered over the Emperor Seamounts, but including the NWHI, and 20–30% shallower north of 45°N, particularly in the Gulf of Alaska (Figs 3 and 4). The MLT was 0.5–1°C lower over the Emperor Seamounts and 0.5–1°C higher in the Gulf of Alaska during winter and spring 1977–88, compared to the same seasons 1960–76. Those MLT changes are consistent with the MLD changes, in that deeper MLD corresponds to mixing of lower temperature water into the mixed layer. This consistency check gives us further confidence that the MLD estimates that we have computed reflect real changes rather than instrumental problems. The mean winter MLD cumulative frequency distributions for all three regions show that the change in mean MLD is the result of a shift in the entire MLD frequency distribution and not due to a change in some extreme values (Fig. 5).

The 1960–76 mean monthly MLD and MLT used as model input show typical seasonal patterns (Fig. 6). The 1960–76 annual cycle of model output for mixed layer nitrogen, phytoplankton and herbivorous zooplankton densities and production shows regional differences (Fig. 7). Mixed layer nitrogen remains high throughout the year in the Gulf of Alaska, is generally depleted at the Seamounts, and is continually depleted in the NWHI (Levitus *et al.*, 1993). Phytoplankton density is essentially constant in all three regions, at levels consistent with observations (Fasham, 1995; Winn *et al.*, 1992; Venrick *et al.*, 1987).

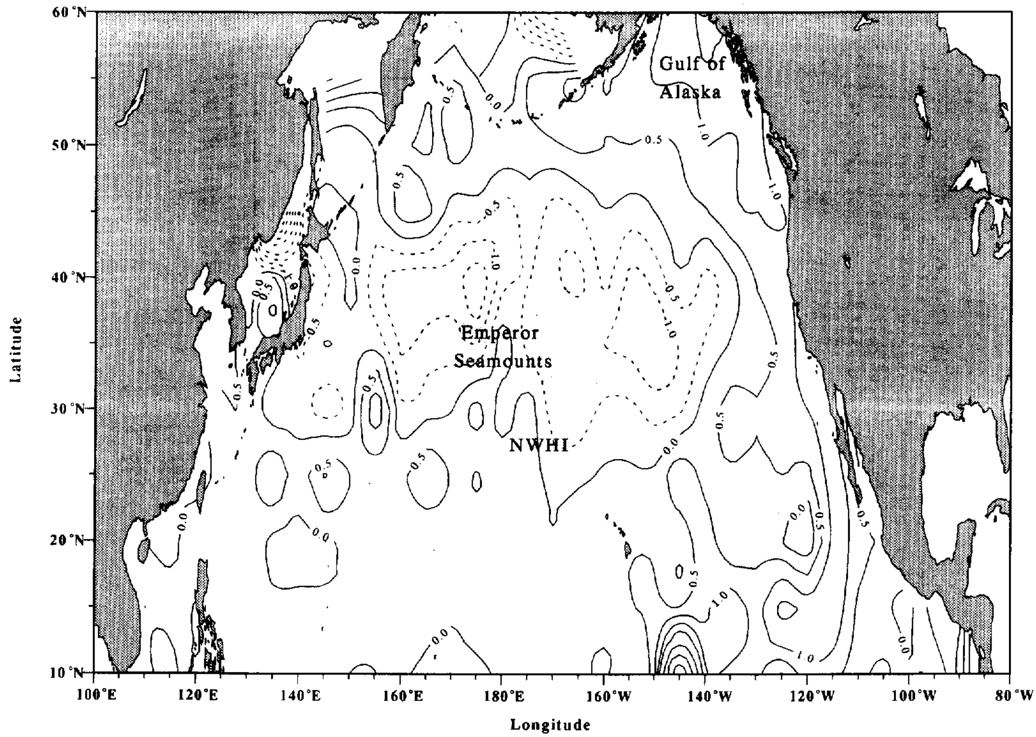


Fig. 4. Change in °C mean winter and spring MLT between 1977–88 and 1960–76. Shading for 1977–88 MLT which are more than 0.5°C colder than 1960–76 MLT. Dashed contours are negative values.

Comparison of model outputs to field data will use the conversion 1 mmol N = 80 mg C and 1 mg Chl = 1.6 mmol N which are derived from a Chl:C mass ratio of 1:50, a C:N mole Redfield ratio of 6.625, and the 12 g molecular weight for carbon. Model phytoplankton biomass values for the NWHI from 0.1–0.2 mmol N/m^3 are consistent with field observation of 0.06–0.2 mmol N/m^3 (Venrick, 1987) and model estimates for the Gulf of Alaska from 0.15–0.35 mmol N/m^3 are within the range for field values of 0.1–1.0 mmol N/m^3 (Hood and Zimmerman, 1986; Fasham, 1995). Unlike chlorophyll for phytoplankton, there is no measure of herbivorous zooplankton to evaluate model output for all three regions. However, the model's annual cycle of herbivorous zooplankton density, constant in NWHI and seasonal for the Emperor Seamounts and Gulf of Alaska, are consistent with observations on zooplankton patterns but, at least for the Gulf of Alaska, the model density may be too high (Fig. 7) (Fasham, 1995; Frost, 1993). However, since we are concerned with differences in production rather than absolute abundance levels, the high model values of herbivorous zooplankton biomass may not be a serious problem. A 95% confidence interval for daily primary production offshore of the Hawaiian Islands integrated to 200 m is 2.5–9.4 mmol N/m^3/day 200–750 mgC/m^2/day) which yields a primary production density of 0.01–0.05 mmol N/m^3/day (Karl *et al.*, 1995). The model values ranging from 0.01–0.02 mmol N/m^3/day are within the lower end of this confidence interval (Fig. 7). For the Gulf of Alaska, daily primary production integrated to 80 m

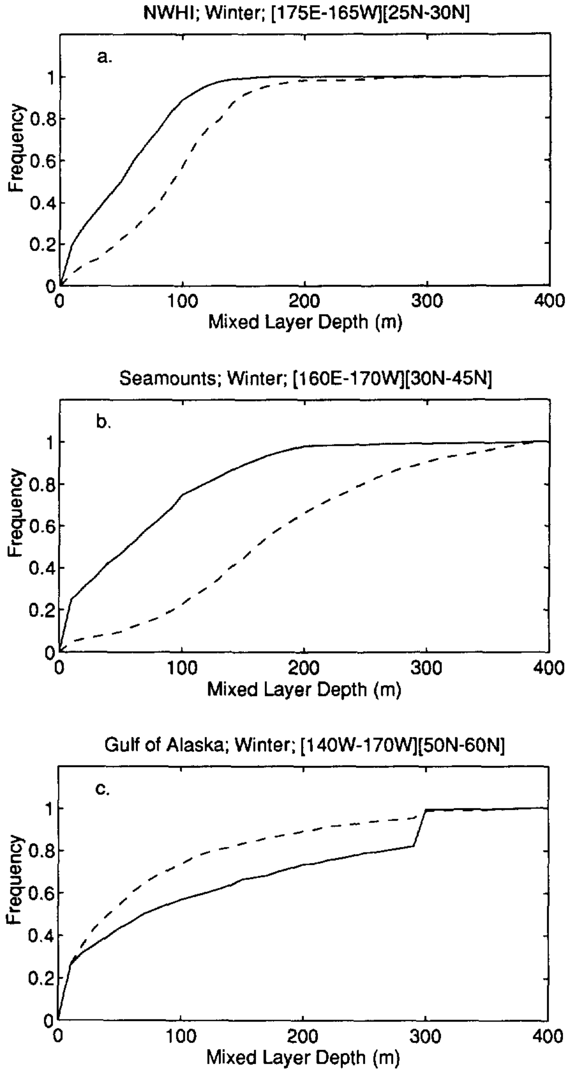
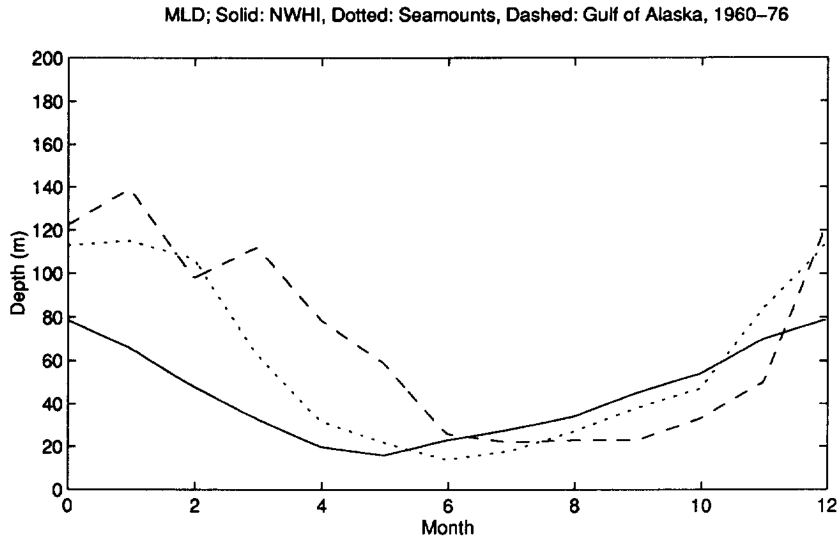


Fig. 5. Cumulative frequency distributions for winter MLD for 1960–76 (solid line) and 1977–88 (dashed line). (A) NWHI (B) Emperor Seamounts (C) Gulf of Alaska.

during May–September ranged from 4.5–17.8 mmol N/m^2/day (358–1420 mgC/m^2/day) which corresponds to densities ranging from 0.06–0.2 mmol N/m^3/day (Welschmeyer *et al.*, 1993). The model values of 0.1–0.13 mmol N/m^3/day fall within this range (Fig. 7).

The changes, all relative to 1960–76 values, in 1977–88 monthly MLD, nutrients, primary and secondary production derived from the model with 1977–88 MLD show regional differences (Fig. 8). In the NWHI during 1977–88 MLD deepened by up to 50% largely during the first quarter of the year, resulting in a doubling of nitrogen in the euphotic zone and increases of 50–200% in daily primary and secondary production during the first quarter (Fig. 8). Over the Emperor Seamounts MLD was also deeper by 30–80%

(A)



(B)

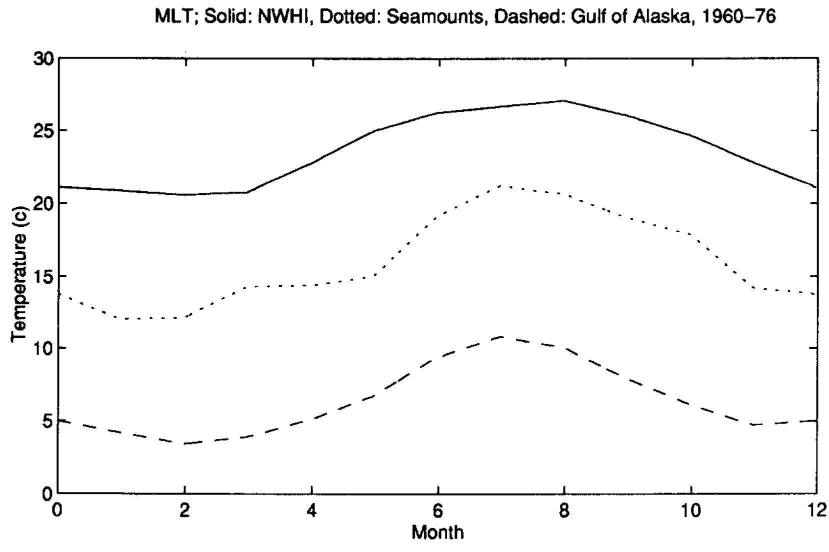


Fig. 6. (A) monthly MLD (B) monthly MLT for 1960–76 for NWHI (solid line), Emperor Seamounts (dotted line) and Gulf of Alaska (dashed line).

for 8 months during 1977–88 (Fig. 8). The deeper MLD elevated nitrogen in the euphotic zone but resulted in 30% lower primary and secondary production during the winter quarter and about 20% higher production during the spring quarter (Fig. 8). In the Gulf of Alaska, MLD during 1977–88 was 30–40% shallower during the first half of the year compared to 1960–76, resulting in as much as 50% more primary production and up to 150% more secondary production during the first half of the year (Fig. 8).

The sensitivity results are shown in Table 2 along with the baseline run, which is the sum

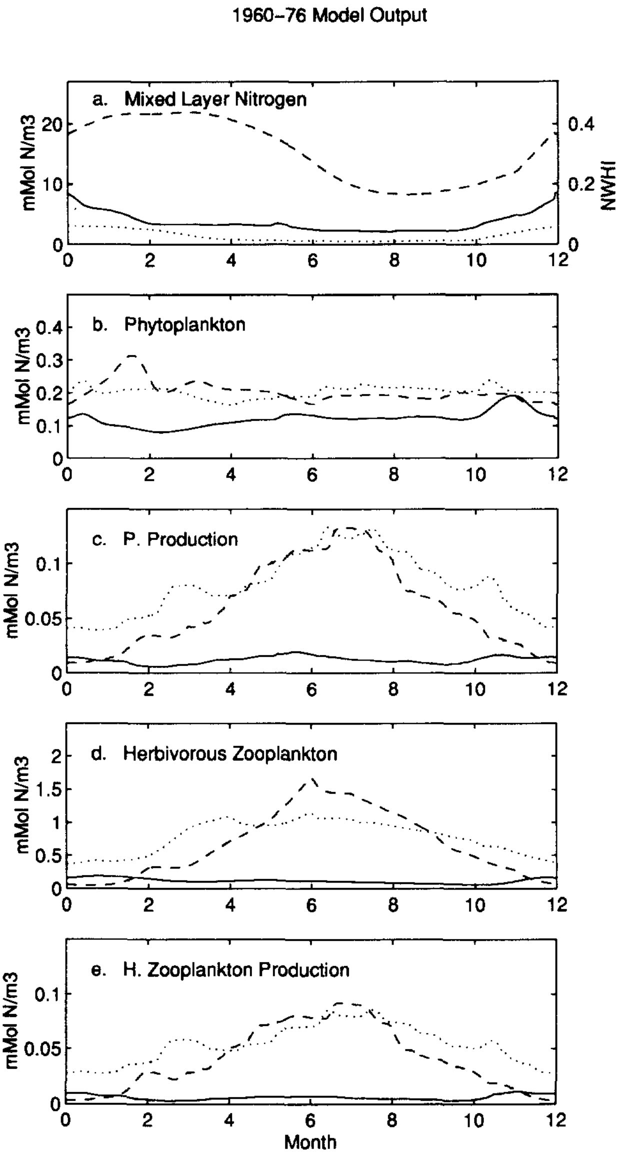


Fig. 7. Model output for 1960–76 for NWHI (solid line), Emperor Seamounts (dotted line), and Gulf of Alaska (dashed line). (A) mixed layer nitrogen. (B) phytoplankton density. (C) phytoplankton production (D) herbivorous zooplankton density. (E) herbivorous zooplankton production.

of the model results for phytoplankton covering January–June from Fig. 8. There are five cases where changes in nutrient or light parameters changed baseline results by more than 25% (Table 2). The model results for the Emperor Seamounts are sensitive to changes in both nutrients and light parameter (Table 2). The other case is for the Gulf of Alaska, where model results are sensitive to an increase in light parameter values (Table 2). Thus,

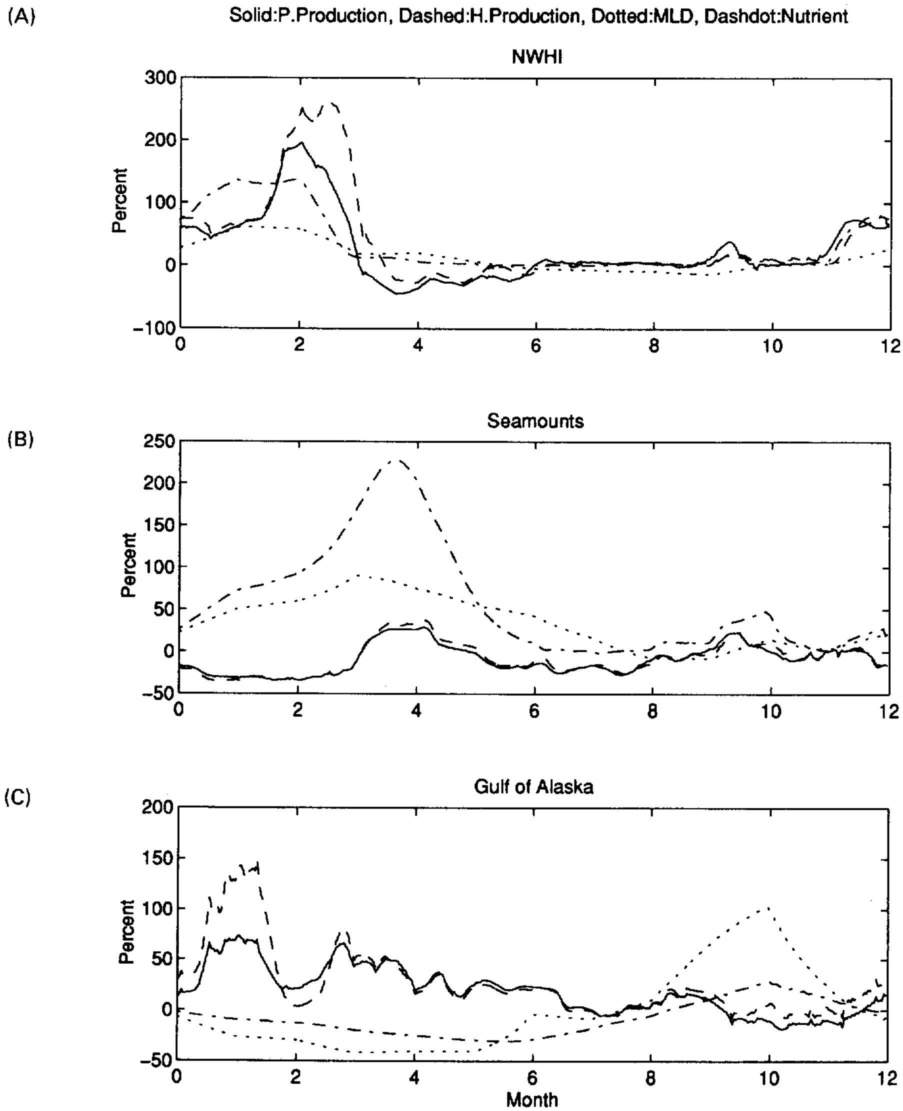


Fig. 8. Percent change in monthly MLD (dotted line), MLD nitrogen (dash dot line), primary production (solid line) and herbivorous zooplankton production (dashed line) for 1977–88 relative to 1960–76. (A) NWHI (B) Emperor Seamounts (C) Gulf of Alaska.

the effects of changing MLD are least sensitive to parameter changes at the extremes of the latitude range, and most sensitive in the transition.

DISCUSSION

Decadal-scale ecosystem changes have been described in both the NWHI and Gulf of Alaska and will be compared to results from our model simulation. Unfortunately, while many fisheries resources are harvested from the transition zone, we were unable to find information on changes of abundance of marine resources from the Emperor Seamounts

Table 2. Percent change in phytoplankton production, January–June 1977–78 *relative to January–June* 1960–76 *levels*

Run	NWHI	Emperor Seamounts	Gulf of Alaska
Baseline	44	−12	43
25% increase in deep nutrients	42	−16*	43
25% decrease in deep nutrients	48	−6*	43
25% increase in light parameters	34	−18*	83*
25% decrease in light parameters	43	−5*	36

*Values differing from baseline run by more than 25%.

region. Fisheries data does exist on catches at the Emperor Seamounts of the pelagic armorhead (*Pseudopentaceros wheeleri*), but this fish migrates between the transition zone and the Gulf of Alaska and hence armorhead abundance may not be a good indicator of the productivity at the seamounts.

In the NWHI, observed changes of 60–100% over baseline levels in productivity for lobsters, sea birds, reef fishes, and monk seals have been observed and attributed to deeper MLD during 1977–88 (Polovina *et al.*, 1994). This is consistent with the level of increase in primary and secondary production calculated from the observed MLD change and the plankton model. For the northern subtropical gyre, it appears that additional nutrients obtained from deep MLD enhance production in spite of the reduction in mean light levels in the deeper MLD.

In the Gulf of Alaska there are considerable biological data showing higher fish and zooplankton densities during the late 1970s and 1980s compared to earlier decades, as well as correlations between biological indices and an index of the strength of Aleutian Low Pressure System (McFarlane and Beamish, 1992; Beamish and Bouillon, 1993; Brodeur and Ware, 1992). Indices of abundance for summer zooplankton, some pelagic fishes, and squids indicate biomass levels during 1980–89 were double those in 1956–62 (Brodeur and Ware, 1992). Trends in North Pacific salmon production follow changes in the Aleutian Low Pressure Index from 1925–89 (Beamish and Bouillon, 1993). Above average North Pacific salmon catches occurred during 1925–45 and 1977–89, when the Aleutian Low Pressure System was more intense than average, while below average salmon catches occurred during 1946–76 when the Aleutian Low was weaker than average. Likewise, a significant correlation has been observed between zooplankton, particularly copepod, abundance during May–March at Ocean Station P in the Gulf of Alaska and the intensity of the Aleutian Low Pressure System for the period 1965–81 (Beamish and Bouillon, 1993; McFarlane and Beamish, 1992). The link between the Aleutian Low Pressure Index and copepods is thought to be the reason for the coherence between the Aleutian Low Pressure and salmon production since salmon feed both directly on copepods and on fish which feed on copepods (Beamish and Bouillon, 1993).

The link between the Aleutian Low Pressure System and zooplankton is not known, but our MLD analyses and simulation of plankton production suggest the link is through the change in MLD. During 1977–88, when increases in salmon and zooplankton were observed in the Gulf of Alaska, our analyses found an intensification of the Aleutian Low led to a shallower MLD in the Gulf of Alaska resulting in increased plankton production. The observed changes in MLD and simulations of the plankton model are consistent with these observed biological changes. The shallower MLD of up to 50% during winter and spring 1977–88 are shown, based on the model simulation, to result in a 50% increase in primary and secondary production for up to 8 months. Hence, in the subarctic gyre, light appears limiting to production, and shallower MLDs result in high production.

The sensitivity analyses conclude that increased production resulting from the 1977–88 MLD change is robust to changes in light and deep nutrient input parameters in the NWHI and Gulf of Alaska. However, the magnitude of the increase in the Gulf of Alaska is particularly sensitive to light availability. Consistent with both nutrient and light-limiting production at the Emperor Seamounts, the magnitude of the decline in production at Emperor Seamounts due to 1977–88 deeper MLD depends more critically on both light and deep nutrient levels.

The 1977–88 climate event in the central and North Pacific substantially altered MLD, and the ocean ecosystem responded to this change. Although there are gaps in the data and simplifications in the model, the results we have are all consistent with the idea that the subarctic is light-limited while the subtropic is nutrient-limited. In between is a region balanced between the two limitations, more complicated than our models or observations can resolve. Finally, we've focused only on the impact of the 1977–88 climate event on MLD. Changes in other processes with biological significance such as ocean circulation or atmospheric input of iron may have also occurred but are beyond the scope of this paper.

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